Interactions between tadpoles of Green and Golden Bell Frog *Litoria aurea* and Striped Marsh Frog *Limnodynastes peronii*

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ABSTRACT

Abstract: Experiments with tadpoles have been used to distinguish between intra- and inter-specific interactions and between interactions that arise through direct physical contact or indirectly through water-born movement of chemicals or micro-organisms. In the case of two Australian frog species, the Green and Golden Bell Frog *Litoria aurea* and the Striped Marsh Frog *Limnodynastes peronii*, it has been suspected that there are negative chemical interactions between the tadpoles of these two species, and that management of the former species, which is considered 'threatened' with extinction, may have to consider such interactions. We therefore sought to evaluate the nature of any interactions between tadpoles of these two species using three experimental treatments in which each tadpole species occurred on its own (i.e., "separate"), in the same water as the other species but separated by a mesh partition (i.e., "adjacent"), and intermingling together in the same water (i.e., "mixed"). We minimized any effects of coprophagy through the use of a mesh that was below the tadpoles and through which the faeces settled and became unavailable.

We found that: (a) *L. aurea* tadpoles grew faster but developed more slowly than *Lim. peronii* tadpoles; (b) for both frog species, tadpoles grew more slowly in the "adjacent" treatment than in the "mixed" or "separate" treatments, but there was no significant difference between these latter two treatments; and (c) treatment had no apparent effect on tadpole survival or development for either species. These results indicate that there were no differences between the effects of intra- and inter-specific interactions on either growth or development when tadpoles were allowed to intermingle. It is difficult to explain why our "adjacent" treatment was significantly outside the range exhibited by the other two treatments in terms of tadpole growth and there was no clear evidence of any indirect chemically-based interactions between tadpoles of the two species. As this study has provided no indication that there may be inter-specific interactions between tadpoles of *L. aurea* and *Lim. peronii* that are any different from intra-specific interactions, it does not support suggestions that *L. aurea* breeding habitat might be enhanced through modifications that make it less suitable for tadpoles of *Lim. peronii*.

Key words: Australian frogs; Interspecific competition; *Limnodynastes peronii; Litoria aurea;* Tadpoles

Introduction

Negative interactions between larvae of different amphibian species have often been inferred or detected, and may be important in determining patterns of species coexistence and community structure. For example, the larvae of some amphibian species prey on the larvae of other species (Holbrook and Petranka, 2004; Sredl and Collins, 1991). Competition between larvae of different species may also occur, with the presence of one species adversely affecting survival, growth or development of the larvae of another species (Banks and Beebee, 1987; Bardsley and Beebee, 1998, 2001a, 2001b; Griffiths, 1991; Griffiths et al., 1993; Kiesecker and Blaustein, 1998; Kupferberg, 1997; Skelly, 1995; Woodward, 1982). Interactions between larvae of different species may influence the nature and extent of other operating factors, such as when predation by one amphibian species affects the magnitude of competition or when behavioural interactions between species influence exposure to abiotic factors (Holbrook and Petranka, 2004; Morin, 1981; Morin, 1986, 1995; Odendaal and Bull, 1983; Peacor and Werner, 1997). The outcome of interactions between larvae of different amphibian species may be affected by other factors such as physico-chemical properties of the aquatic environment or the level or distribution of available food (Griffiths et al., 1993; Kiesecker et al., 2001; Warner et al., 1991). Interactions between amphibian larvae have been found to affect niche separation and relative abundances of coexisting species, and patterns of community structure (Banks and Beebee, 1987; Bardsley and Beebee, 1998; Kiesecker et al., 2001).

Such negative effects of one amphibian species on another may occur through a variety of mechanisms, and may be the result of either direct or indirect interactions between animals. Direct interactions include predation (see above) and aggression (Faragher and Jaeger, 1998). Indirect interactions include reduced access to food and other resources (Kiesecker et al., 2001), and 'interference' through the production of chemicals or faecal algae that inhibit survival, growth or development (Bardsley and Beebee, 1998, 2001a; Faragher and Jaeger, 1998; Griffiths et al., 1993; Wong et al., 2000).

Observations and experiments may help to differentiate between these different mechanisms. Observations may, for example, enable differences to be determined between the behaviour of one species in the presence or absence of another (Faragher and Jaeger, 1998; Kiesecker et al., 2001; Kupferberg, 1997). Experiments where physical contact between two species is restricted, as for example when a partition may separate two species that none-the-less occur within the same water body, may permit certain direct and indirect effects to be distinguished (Bardsley and Beebee, 2001a; Bardsley and Beebee, 2001b; Griffiths, 1991; Griffiths et al., 1993). Experiments where direct physical contact is eliminated, but the larvae of one species occur in water previously used by another, can further differentiate between effects (Faragher and Jaeger, 1998).

In the case of two Australian frog species, the Green and Golden Bell Frog *Litoria aurea* and the Striped Marsh Frog *Limnodynastes peronii*, it has been suspected that there are negative chemical interactions between the tadpoles of these two species, and that management of the former species, which is considered 'threatened' with extinction, may have to consider such interactions (A. White, pers. comm.). There is widespread opportunity for interactions between tadpoles of these two frog species as *Lim. peronii* occurs at more than 80% of sites in NSW where *L. aurea* is present (Pyke and White, 1996) and, at sites where both species occur, the two species are commonly found intermingling together in the same water body (Pyke and White unpubl.). Some observations and a pilot experiment have suggested, furthermore, that tadpoles of *Lim. peronii* may adversely affect the survival, growth and development of *L. aurea* tadpoles through chemical interaction (Pyke and White, 1999; A. White, pers. comm.). At a number of ponds, for example, a simultaneous increase in abundance of *Lim. peronii* and decrease for *L. aurea* have been observed (Pyke and White, 1999). *Litoria aurea* is considered 'endangered' in New South Wales and 'vulnerable' both in Victoria and nationally (Pyke and White, 2001), and management of this species could therefore include actions designed to reduce any negative impacts from tadpoles of other frog species (e.g., modify breeding habitat so that it becomes less suitable for other frog species that negatively affect this species).

The aims of the present study were therefore to use laboratory experiments to (a) evaluate possible effects that the presence of tadpoles of one of these frog species may have on survival, growth and development of tadpoles of the other species; (b) determine the extent to which any such observed effects are caused by chemically-mediated interactions between tadpoles; and (c) consider the extent to which the results of these experiments may be extrapolated to the wild.

Methods

Animal Collection

We obtained tadpoles of *L. aurea* from a single egg mass that was laid at Sydney's Taronga Zoo (as part of a *L. aurea* captive breeding program) on 4 December, 2001. Due to the conservation status of *L. aurea*, tadpoles could not be obtained from the wild, and more than one egg mass could not be obtained due to the limited supply and high demand for use in translocation efforts. Tadpoles of *Lim. peronii* were obtained from *Lim. peronii* egg clutches collected within 12 hours of deposition on 4 December, 2001 at Burnt Bridge Creek in the Sydney suburb of North Balgowlah. As *Lim. peronii* egg masses contain fewer eggs than those of *L. aurea*, we collected three to provide similar egg numbers for each species. These egg masses were mixed to minimise genetic variation among treatments. We maintained *L. aurea* and *Lim. peronii* eggs and tadpoles without disturbance in separate holding aquaria until atrophy of external gills (Gosner stage 25; 10 December, 2001). They were then transferred to experimental containers (see below). We assume that the low numbers of egg masses (i.e., 1 for *L. aurea* and 3 for *Lim. peronii*) did not affect the results.

Treatment Aquaria and Experimental Design

The experiment was conducted in two adjoining constant temperature (CT) rooms in the Biological Science Building, University of New South Wales in the Sydney suburb of Kensington. Throughout the experiment, both rooms were maintained at 21ºC, with a photoperiod of 12:12.

Tadpoles were raised in an array of Perspex aquaria (22 x 17 x 17 cm deep), each containing five litres of dechlorinated tap water. In order to prevent direct contact, but allow possible indirect contact between tadpoles, aquaria were divided in half by placing a black nylon mesh basket (1 mm mesh size) with a central division into each aquarium. This division prevented physical contact between tadpoles in separate sections, but allowed water, dissolved chemicals and some food matter to flow through. This division would have restricted, but not completely eliminated, visual contact between tadpoles in separate sections. The floor of the mesh basket was raised approximately 5 mm from the base of each aquarium, allowing tadpole faeces to fall through the mesh, thus reducing coprophagy and consequent reductions in growth and development from unicellular algae that may be present in the faeces (Baker and Beebee, 1997; Bardsley and Beebee, 2001b; Beebee, 1991; Beebee and Wong, 1992; Steinwascher, 1978). We placed six tadpoles in each section, resulting in 12 tadpoles per aquarium, or 2.4 tadpoles per litre. This density is within the range of natural densities observed in the field for both species (e.g. up to 10 *L. aurea* tadpoles and up to 15 *Lim. peronii* tadpoles per litre at Broughton Island, NSW, G. H. Pyke, unpublished data; up to 21 *Lim. peronii* tadpoles per litre in Sydney, NSW; (Mokany and Shine, 2002)).

The species of tadpoles placed in each aquarium varied according to experimental treatment. There were four experimental treatments as follows: (i) *Separate L. aurea:* Six *L. aurea* tadpoles in each section (ii) *Separate Lim. peronii:* Six *Lim. peronii* tadpoles in each section. (iii)

Adjacent: Six *L. aurea* tadpoles in one section and six *Lim. peronii* tadpoles in the other. (iv) *Mixed:* Three *L. aurea* tadpoles and three *Lim. peronii* tadpoles in each section.

There were ten replicate aquaria per treatment, which were placed into one of two spatial blocks which were set up on the floor of the two CT rooms, with one block in each room. Due to space limitations, six replicates of each treatment (24 aquaria) were randomly chosen and placed in one room, and four replicates (16 aquaria) in the other.

A strategy similar to that used in other studies (Pakkasmaa and Aikio, 2003) was adopted to ensure that tadpole densities remained constant and hence that density was not a confounding factor in our experiments. An extra four replicates of each treatment were placed in the larger CT room and any tadpoles that died in experimental aquaria were replaced by tadpoles randomly selected from these extra aquaria. After week 4, however, these replacement tadpoles were, for unknown reasons, all conspicuously smaller (approximately 30% smaller) and less developed than any of the experimental tadpoles and, within experimental aquaria, the numbers of these distinctly smaller tadpoles remained constant and equal to the numbers of replacement tadpoles. We therefore assume that these smaller, less developed tadpoles were always the replacement ones and omit them from the analyses below. As a 30% difference in size between tadpoles may have little or no effect on the outcome of competitive interactions (Werner, 1992) and the average number of replacement tadpoles did not differ significantly across treatments (see below), we also assume that they contributed to tadpole density in the same manner as the other tadpoles and do not differentiate between aquaria in terms of how many such replacement tadpoles there were. On the other hand, prior to week 4 there were no clear differences in body size between the replacement and experimental tadpoles and so we do not differentiate between experimental tadpoles and tadpoles that were used as replacements before week 4.

The growth and development experiment commenced on 10 December 2001 (day 0) when tadpoles of each species were removed from the holding aquaria with a dip-net and placed into the appropriate experimental aquaria. All tadpoles were of the same size and developmental stage (4 mm snout-vent length, Gosner stage 25). On day 3, any dead tadpoles in treatment and extra aquaria were removed and replaced with tadpoles from the holding aquaria. Thereafter, any dead tadpoles in treatment aquaria were replaced with tadpoles from the extra aquaria obtained from the same treatment that they were being added to. As tadpoles were removed from, or died in extra aquaria, remaining back-up tadpoles were redistributed to maintain tadpole density. Water volume was reduced proportionally in back-up aquaria if there were fewer than twelve tadpoles per aquarium.

Tadpoles in each aquarium section were fed approximately 5 g of boiled lettuce every 1-2 days and 0.5 g of Hikari™ Algal Wafers every two-weeks. Uneaten food particles and most faeces were removed prior to food addition. Two litres of water from each tank was removed weekly and replaced with tap water dechlorinated with 5 ml/250 L Wardley® Tri-Start™. pH in experimental aquaria ranged from 6.5-7.5.

Tadpole Growth, Development and Survival

The response variables measured were survival, tadpole body-size, and tadpole developmental stage. Tadpole body size was measured in terms of SVL (mm), and developmental stage was recorded as Gosner stage number (Gosner, 1960). Survival refers to the percent of tadpoles placed in treatment aquaria days 0-3 that were alive at the termination of the experiment. SVL and Gosner stages of tadpoles were determined at day 0 and at weekly intervals throughout development.

Data Analysis

We restricted our analyses to the period up to week 7 as the tadpoles began metamorphosing after this time. Such metamorphosis would have depended on body size and developmental stage, and it occurred at unequal rates amongst aquaria. Once it began, it would therefore have contributed additional variation to the experiment and confounded results.

Statistical analyses were based on the mean SVL and mean Gosner stage for each species within each tank at each weekly measurement time. This ensured that observations made at a particular time were independent. As the frequency distributions for both means were generally unimodal, roughly symmetrical in shape and had relatively low variance, it was assumed reasonable to use parametric statistics that assumed Normal distributions for such observations. The following analyses were therefore possible, with a probability threshold of 0.05 adopted for statistical significance.

In our analyses the dependent variables were the observed means (i.e., SVL and Gosner), the independent variables were treatment and frog species and the interaction between them, and, wherever possible, we used Repeated Measures Analysis of Variance (i.e., REM ANOVA) across the weekly observations. However, such analysis was considered inappropriate when there were significant interactions between some variables and the time variable (i.e., week) raised to a power of order 2 or higher. Under such circumstance it would presumably have been possible to test for effects of the independent variables after first fitting a polynomial relationship with the time variable, but such analysis proved unnecessary (see below). On this basis, the REM ANOVA was carried out for the first 2-3 weeks and for weeks 6-7, and was therefore equivalent in some situations to a paired t-test between successive weeks. In addition, normal ANOVA was carried out for some specific weeks of interest.

A Kaplan-Meier product limit estimator (Pollock et al., 1989) was used to analyse survival over time. Due to the higher mortality of replaced versus original tadpoles in each tank (Log-rank test, $P<<0.001$), tadpoles added to aquaria after week four were excluded from further analysis. Estimated survival functions were compared by the log rank test in order to determine if they could have come from the same underlying true-survival curve.

Results

In our experiments, *L. aurea* tadpoles grew faster but developed more slowly than *Lim. peronii* tadpoles (Figs. 1 & 2). At the start of the experiments (i.e., weeks 1-2), the average SVL for the *L. aurea* tadpoles was significantly less than that for the *Lim. peronii* tadpoles (F=8.3; df=1, 80; P=0.005; REM ANOVA), but the growth rate was consistently higher for *L. aurea* after that (Fig. 1) and, by weeks 6 and 7, the *L. aurea* tadpoles were significantly longer than the *Lim. peronii* tadpoles (F=26.0; df=1, 89; P<0.001; REM ANOVA). At the start of the experiments (i.e., weeks 1-3), there was no significant difference in Gosner developmental stage between tadpoles of the two species (F=0.5; df=1, 72; P=0.48; REM ANOVA), but, thereafter, the development rate was consistently higher for *Lim. peronii* tadpoles (Fig. 2) and, by weeks 6 and 7, the average Gosner stage was significantly higher for the *Lim. peronii* tadpoles than for the *L. aurea* tadpoles (F=46.2; df=1, 89; P<0.001; REM ANOVA).

For both frog species, tadpoles grew more slowly in the "adjacent" treatment than in the "mixed" or "separate" treatments, but there was no significant difference between these latter two treatments and, for graphical presentation, the latter two treatments are therefore combined (Fig. 1). For weeks 1-2 the *L. aurea* tadpoles in the "adjacent" treatment grew significantly more slowly (F=12.5; df=2, 35; Fig.1; P<0.001, REM ANOVA) than those in the other two treatments, which were not significantly different from one another (F=0.4; df=1, 35; P=0.52; REM ANOVA). Over this same period there was a significant interaction between week, species and treatment but no significant effect of treatment on the growth rate of *Lim. peronii* tadpoles (F=4.0; df=2, 78; P=0.02 for interaction between week, species and treatment, REM ANOVA; F=2.8; df=2, 78; P=0.07 for treatment effect when *Lim. peronii* considered on its own, REM ANOVA). For weeks 6-7 there were no significant interactions involving species and treatment (F=0.8; df=2, 90; P=0.43 for species x treatment interaction, F=0.5; df=2, 90; P=0.63 for week x species x treatment interaction, REM ANOVA), no significant difference in tadpole growth rate between the "mixed" and "separate" treatments (F=0.3; df=2,90; P=0.74; REM ANOVA), and the tadpole growth rate was significantly lower for the "adjacent" treatment than for the other two treatments (Fig. 1, F=4.7; df=1, 93; P=0.03; REM ANOVA). Over the course of the experiments, the tadpole growth rates in the "adjacent" treatment were lower than those in the other two treatments combined for both frog species (Fig. 1) and by weeks 6 and 7 average SVL was significantly lower in the "adjacent" treatment than in the other two combined for each frog species (Fig. 1, F=6.0; df=1, 92; P=0.02, REM ANOVA). Strangely, all treatments for both species converged at week 3 with no significant effect of treatment at this time (Fig. 1, F=0.3; df=2, 82; P=0.71 for treatment x species interaction, F=0.0; df=2,82; P=1.00 for treatment, ANOVA).

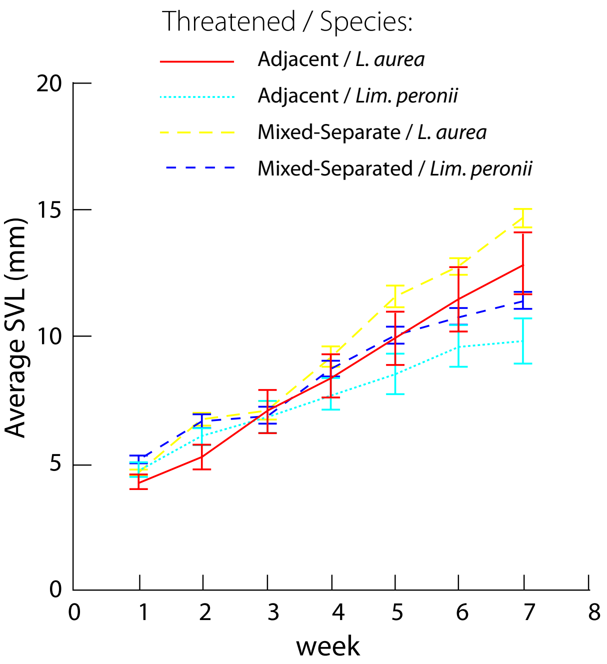

Figure 1. Average SVL (mm) vs week for Treatment (i.e., "Adjacent" vs "Mixed"-"Separate" Combined) and each species

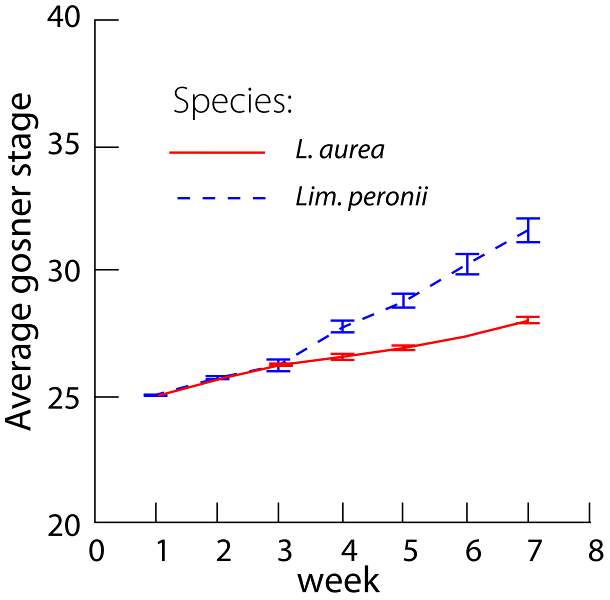

Figure 2. Average Gosner stage vs Week for *L. aurea* and *Lim. peronii*

Treatment had no apparent effect on tadpole development for either species. For the first 3 weeks, there was a significant effect of week (F=87.5; df=2, 146; P<0.001; REM ANOVA) , indicating, as mentioned above, that development had progressed during this period, but none of the other effects or interactions were significant (P's>0.17, REM ANOVA). For weeks 6-7 there were, as already mentioned, significant differences between the two species (Fig. 2), but no other significant effects or interactions (P's>0.05, REM ANOVA).

Mean survivorship over time was higher for *Lim. peronii* tadpoles than for *L. aurea* tadpoles , but did not differ significantly with treatment (and hence neither did the number of replacement tadpoles; Table 1). Survival in each treatment ranged from 83-92% for *Lim. peronii* and 55-68% for *L. aurea*, with most *L. aurea* mortality occurring in the first three weeks.

Table 1. The effect of treatment and species on the survival of *L. aurea* and *Lim. peronii* tadpoles (Log-Rank Test).

	Comparison	χ^2	P
Treatment	*L. aurea* vs *Lim. peronii*	52.6230	<0.001
L. aurea	Separate vs Adjacent	0.5462	>0.25
	Separate vs Mixed	3.453	>0.05
	Adjacent vs Mixed	1.4518	>0.10
Lim. peronii	Separate vs Adjacent	0.1732	>0.50
	Separate vs Mixed	2.9909	>0.05
	Adjacent vs Mixed	1.1544	>0.25

Discussion

The differences in rates of growth and development between tadpoles of *L. aurea* and *Lim. peronii* could be related to other differences between these two species. Compared with *Lim. peronii*, *L. aurea* matures at a longer and heavier size, and shows reversed sexual dimorphism in adult size (i.e., adult males smaller than adult females) (Moore, 1961). The average number of eggs per spawning is relatively large in both species, but greater for *L. aurea* than for *Lim. peronii* (Hengl and Burgin, 2002; Pyke and White, 2001). However, possible explanations for such differences have not been published.

It is difficult to separate effects on growth and development of amphibian larvae from effects on survival, because the size and developmental stage of an animal may affect its likelihood of survival. If, for example, mortality amongst a group of tadpoles tended to occur within a certain size range then surviving (and hence measured) tadpoles might change in average size without any change in the size of each individual. In our case, there was no apparent effect of treatment on survival and we tried to compensate for mortality through replacement of dead individuals and adjustments to water volume, but we cannot rule out biases of the sort described above. Indeed, the high mortality of *L. aurea* tadpoles during the first 3 weeks might explain why the treatments converged in terms of SVL for this species at week 3 (Fig. 1). Interspecific effects on larval survival, growth and development have been examined experimentally in many other amphibian studies (Griffiths, 1991; Holbrook and Petranka, 2004; Kiesecker and Blaustein, 1998; Morin, 1986; Warner et al., 1991; Warner et al., 1983), but none has apparently considered possible interactions amongst these effects. One possible way to do this would be to use marked or recognizable tadpoles in pairs with different water volumes used to simulate variation in density, but this would necessitate large initial numbers of replicates to allow for the inevitable and possibly high mortalities, and such a study has not apparently been carried out.

Differentiating direct and indirect interactions between amphibian larvae is only possible through experiments in which different larvae use the same water but otherwise have restricted contact with one another, yet such experiments have so far been rare. In our study and in two others, physical contact between groups of tadpoles was prevented in one treatment through the use of a mesh barrier through which water could pass, but not tadpoles (Bardsley and Beebee, 2001a; Griffiths, 1991). In these studies, there could have been some visual interaction across the barrier. In two studies, tadpoles of one species were placed in water that had previously been 'conditioned' through use by another species, and so there was no direct contact between these two species in this situation (Faragher and Jaeger, 1998; Griffiths, 1991).

Distinguishing between different kinds of indirect interactions is only possible through further modification to the experimental protocols. In our study, for example, the extent of coprophagy was restricted through the provision of a mesh that was near the bottom of each tank and impenetrable to tadpoles, and through which faeces would have settled and become unavailable. In this situation, any effects of coprophagy should have been minimal. On the other hand, in the other two similar studies, faeces were retained and could pass through the mesh that separated groups of tadpoles (Bardsley and Beebee, 2001a; Griffiths et al., 1993).

A number of studies, including the present one, have experimentally contrasted inter- and intra-specific interactions between amphibian larvae by comparing survival, growth or development in water-bodies containing different species on their own with water-bodies containing two intermingling species, but results have varied. Inter-specific effects exceeded intra-specific effects in some cases and, when it occurred, was generally asymmetrical with one species showing less effect than the other (Bardsley and Beebee, 2001a; Bardsley and Beebee, 2001b; Faragher and Jaeger, 1998; Griffiths, 1991; Kupferberg, 1997; Odendaal and Bull, 1983). In one study, the effects of intra-specific interactions exceeded inter-specific effects (Skelly, 1995) and, in another, the relative effects depended on the pH of the aquatic environment (Warner et al., 1983). In our study, there were no apparent differences between the effects of intra- and inter-specific interactions when tadpoles were allowed to intermingle, as there were no significant differences between the "mixed" and "separate" treatments.

The results of our study contrast with those of the other studies that included a treatment with restricted physical contact between species. The other two studies that had partial contact between species through provision of a mesh barrier in one of the treatments (i.e., equivalent to our "adjacent" treatment) found that this treatment was intermediate between a treatment with full contact between two species (i.e., equivalent to our "mixed" treatment) and a treatment with just one species (i.e., equivalent to our "separate" treatment) (Bardsley and

Beebee, 2001a; Griffiths, 1991). In addition, both studies found that tadpoles in the "mixed" treatment fared worst in terms of survival, growth and development (Bardsley and Beebee, 2001a; Griffiths, 1991). Consistent with these results, when physical contact between tadpoles was eliminated through the use of 'pre-conditioned' water (as described above) in one of the treatments, there was, in one case, no significant difference between this treatment and a 'control' treatment that was equivalent to our "separate" treatment (Griffiths, 1991). In contrast to results from other studies, our "adjacent" treatment was significantly outside the range exhibited by the other two treatments in terms of tadpole growth.

It is difficult to explain these results and there was no clear evidence of any indirect chemically-based interactions between tadpoles of the two species. A possible explanation would arise if there were direct interactions between tadpoles that promoted growth along with indirect chemically-based interactions that slowed growth, if the magnitudes of these direct and indirect effects were similar, and if the effects of both these interactions were greater between species than within either species. Under these circumstances, tadpole growth in the "mixed" treatment would be similar to that in the "separate" treatment because the direct and indirect inter-specific effects would cancel themselves in the "mixed" treatment, relative to any intra-specific effects. In addition, growth in the "adjacent" treatment would be lower than in the "mixed" treatment because of the elimination of the positive effects of direct interaction while the negative indirect effect remained. There are, however, no known apparent biological mechanisms that could produce such interactions.

This study has provided little or no indication that there may be inter-specific interactions between tadpoles of *L. aurea* and *Lim. peronii* that are any different from intra-specific interactions, and hence does not support suggestions that *L. aurea* breeding habitat might be enhanced through modifications that make it less suitable for tadpoles of *Lim. peronii*. Rather, observations that the abundance of *L. aurea* has declined at ponds while *Lim. peronii* abundance has increased at these ponds (Pyke and White, 1999) could be explained on the basis of habitat changes, such as increased vegetative growth and associated decreased water temperature, that make these ponds more suitable to *Lim. peronii* tadpoles compared to *L. aurea* tadpoles.

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